FURTHER OBSERVATIONS ON THE ETHOLOGY OF ALYSSON CONICUS PROVANCHER (HYMENOPTERA: SPHECIDAE)

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Abstract.—Females of Alysson conicus Provancher were observed nesting in large aggregations in a sandy road and path in the Adirondacks. They were active at ambient temperatures of from 15° to 22°C. Females stored adult Cicadellidae (94% Empoa albicans Walsh) in their nests. From 5 to 12 leafhoppers were placed in the fully provisioned, spherical cells, 1.4 to 6.0 cm beneath the surface. Prey were transported to the nests in flight and held by the beak and body with the wasp's mandibles and legs, respectively. Entrances were left open while provisioning. Prey (61%) were parasitized by dryinid wasps in 1980 prior to capture by A. conicus.

Little is known about the bionomics of the genus *Alysson* in North America. Of the nine species in the Nearctic Region, only *A. melleus* Say has been studied to any extent (Hartman, 1905; Rau and Rau, 1918; Evans, 1966; Kurczewski and Kurczewski, 1971).

Alysson conicus Provancher is one of the less commonly collected species. It ranges throughout the northeastern U.S. from southeastern Canada into Virginia (Krombein, 1979). The only known information on its nesting behavior has been published by O'Brien and Kurczewski (1979). The present report adds considerably more data and complements the behavioral information presented in 1979.

Ecology

We observed A. conicus during August 6–10, 1979 and July 20–25, 1980 at the Cranberry Lake Biological Station of the College of Environmental Science and Forestry, in St. Lawrence Co., N.Y. The wasps occupied a 52 m segment of a sandy road which parallels Sucker Brook (Fig. 1), and a compacted, sandy-clayey path 2 m from the lake shoreline on the opposite side of the Station. Dominant vegetation along these areas comprised sec-



Fig. 1. Nesting habitat of *Alysson conicus* at Cranberry Lake, N.Y., showing 80 marked nests within a 6.0×0.9 m area. Individual nests are denoted by white plastic stakes.

ond-growth stands of northern hardwoods, especially red maple (*Acer ru-brum*), sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), yellow birch (*Betula allegheniensis*), poplar (*Populus tremuloides*), and black cherry (*Prunus serotina*). Herbaceous plants, bracken fern (*Pteris latiuscula*), and grasses grew at the edges of the road and path. The road was shaded during much of the day, and the sand in which the wasps nested was uniformly moist. The daily ambient temperatures at the nesting sites ranged from 15° to 22°C during periods of observation. Temperatures in 1979 were unusually cool at night, plunging once to 7°C. Several cool windy days interspersed with rain in 1979 and periods of heavy rain in 1980 dampened wasp activity.

Females of *A. conicus* were active from 0830 to 1630 h (EDT), being most active on sunny days; however, they carried on some "typical" nesting activities during periods of unfavorable weather. Between 0730 and 1000 h many females remained inside their nests, either in terminal cells or lower parts of their burrows. When removed from their nests, such wasps became active within 20 s.

Males were found in sunny spots within the nesting area or resting on overhanging vegetation along the road between 0930 to 1400 h. Some males were observed lapping honeydew off blackberry (*Rubus* sp.) leaves; others were found on flowers of tall meadow rue (*Thalictrum polygamum*).

No copulation was observed; however, males frequently followed closely behind provisioning females on the ground and hunting females on vegetation.

NESTING BEHAVIOR

Females were aggregative, possibly due to the limited suitable nesting habitat. Distances between conspecific entrances ranged from 2 to 25 cm in dense groups but over 1 m in others. The densest aggregation contained 80 nests within a 6×0.9 m area (Fig. 1). Nest tumuli (276) were marked within a 52×1.8 m stretch of the road in 1980. On the lakeside path, we marked 29 nest entrances within a 16.5×1.5 m area.

Six females were observed excavating burrows between 0830 and 1000 h, and from 1500 to 1600 h. They formed pellets of sand with the forelegs, transferred them backwards to the midlegs, and pushed them into the entrance with the hindlegs. The pygidium often assisted in pushing pellets into the opening. The pellets were then pushed to the side of the entrance, the female rotating in a clockwise direction. Often, after several pellets had accumulated in the entrance, the female would move them to one side, forming an asymmetrical tumulus. As a wasp dug deeper, she took increasingly longer (10–25 s) to deposit the soil in the entrance.

Provisioning females flew into the nesting areas from the surrounding vegetation at a sharp angle. One female, grasping a leafhopper venter-up by its beak and body with her mandibles and legs, respectively, flew from a red maple 1.5 m above ground level to the nest. Within 15 to 30 cm of her entrance, she held the prey venter-up on the ground by its beak (Fig. 2). Females walked in a zig-zag manner near their entrances, dropped their prey just outside, entered, turned around, and pulled the leafhoppers inside head-first. One wasp took 5 min between provisioning trips.

Provisioning wasps were skittish on the ground, and flew away at the slightest provocation, often releasing the prey. Such prey were usually not retrieved by the wasps. Some disoriented females flew in circles above the area until they found their entrance, then retrieved the leafhopper and took it into the nest.

All nests were left open during provisioning. Many nests were easily recognized by their characteristic tumuli (Fig. 3), in the form of a simple conical mound, an elongate-convex mound with the entrance off-center, or a turret. Weathering was important in shaping the tumulus, the oldest ones being either absent or inconspicuous. Dimensions of 33 tumuli varied from 4 to 18 mm high ($\bar{x} = 8.4 \pm 3.1$ mm), and from 10 to 20 mm wide ($\bar{x} = 15.9 \pm 2.3$ mm).

Nest entrances (16) ranged from 1.5 to 2.5 mm in diameter ($\bar{x} = 2.1 \pm 0.2$ mm). Burrows went either straight downward through symmetrical tumuli or obliquely downward through asymmetrical ones (Fig. 4). Unfinished nests

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Figs. 2, 3. 2, Alysson conicus female carrying prey to her nest. 3. Tumulus and nest entrance.

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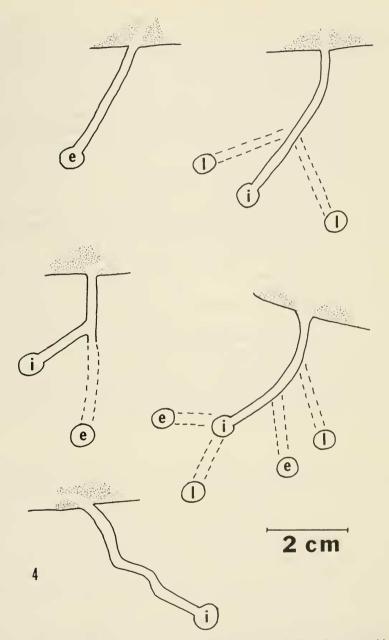


Fig. 4. Side views of *Alysson conicus* nests. Broken lines indicate burrows which could not be traced exactly. Completed cells contained an egg (e) or larva (l). Uncompleted cells are designated by "i."

(20) contained a single terminal cell, but 5 completed or nearly completed nests had from 2 to 5 cells. Cells (34) were spherical (Fig. 4) with a mean diameter of 4.5 ± 0.7 mm (3.0–5.5 mm). Cell depth varied from 1.4 to 6.0 cm ($\bar{x} = 3.8 \pm 1.0$ cm; N = 34) beneath the soil surface. The soil was invariably moist at cell depth.

Prey consisted of adult Cicadellidae, subfamily Typhlocylinae as follows: 218 Empoa albicans Walsh, 2 E. querci Fitch, 2 E. latifasciata Christian, 8 Empoasca atrolabes Gillette, 1 Typhlocyba persephone McAtee, and 1 Ribautiana sp. The prey appeared to be either fully-paralyzed or dead, with no visible appendage or breathing movements.

Fully-provisioned cells, i.e., those with an egg or larva, contained prey placed head-inward and venter-upward. The mean number of prey per completed cell was 8.8 ± 2 (5–12; N = 14). An egg was laid on the uppermost leafhopper in the cell, either to the right or left of center on the sternum as in *A. melleus* (see Fig. 20, Evans, 1966). Four eggs averaged 0.75×0.2 mm. Two cells contained prepupae within ovoidal cocoons, measuring 6.0×2.5 and 5.6×2.3 mm. The cocoons were constructed of silk, sand grains, and leafhopper remains.

There was no evidence of parasitism or predation in 1979. In 1980, however, 61% of the prey were parasitized by dryinid wasps prior to capture by *A. conicus*. Dryinidae are parasitoids of Homoptera, developing at first internally, then extruding through the integument (Krombein, 1979). It is doubtful that there would have been any effect upon *A. conicus* by the dryinid infestation due to the faster development of the *A. conicus* larva. *Alysson conicus* females may have captured parasitized leaf-hoppers because they were less successful than non-parasitized leafhoppers in evading capture.

DISCUSSION

Alysson conicus exhibits the behavioral traits of the genus, as outlined by Evans (1966). It nests in aggregations in cool, moist sandy situations, with females hunting near their nests. Burrows are nearly vertical, with conspicuous, often irregular tumuli. Completed nests are 2- to 5-celled, as in *A. melleus* (Evans, 1966), with the deeper cells in a nest being older.

Although we observed A. conicus females releasing prey outside their entrances and pulling them in, other species of Alysson have been noted carrying prey directly into their nests (Evans, 1966; Tsuneki, 1969). Perhaps many of the entrances at Cranberry Lake were blocked with sand grains, and the females had to clear these away prior to entering.

Alysson conicus prefers Empoa albicans as prey at Cranberry Lake, N.Y. Empoa albicans was common on low vegetation, shrubs, and trees paralleling the nest sites, and the wasps hunted in these areas. Alysson melleus takes a broader range of prey (Evans, 1966). Observations of A. conicus in other areas would undoubtedly reveal differences from the Cranberry Lake population in regards to prey selection.

It is surprising to find A. conicus preying on dryinid infested leafhoppers. This phenomenon has not been noted for any other wasps preying on Homoptera, although it would have been easily overlooked unless the dryinids were extruding through their host's integument.

Alysson conicus nests were shallower than those reported for A. melleus (Evans, 1966) and were less variable in cell depth. The shallower A. conicus nests may reflect the continual, moist sand in perpetual shade, or limitations of the sand layer overlying the compacted organic layer of the road.

ACKNOWLEDGMENT

We thank J. P. Kramer, Systematic Entomology Laboratory, USDA, Washington, D.C. for identifying the prey Cicadellidae.

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